The Fungal Community

Its Organization and Role in the Ecosystem

Second Edition

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Interference Competition

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INTRODUCTION

When there is a simultaneous demand upon the same resource by two populations, and the resource is in insufficient supply to meet the demands of both species, interspecific competition occurs. The major forms of competition in fungi are defined by the types of interactions between competing species. In the earlier edition of this book Professor Lockwood and I attempted to identify and categorize examples of fungal competition either as "exploitation competition" or as "interference competition" (Lockwood, 1981; Wicklow, 1981a), something ecologists have done for larger organisms (McNaughton and Wolf, 1973; Schoener, 1983). With exploitation competition an individual depletes the resource, depriving others of benefits to be gained from those resources, but does not reduce the probability that another individual can exploit the remaining resource pool. In other words, competition for the remaining resource is unaffected. According to Schoener (1983), exploitation competition is the most common form of competition identified in studies of larger organisms.

Interference competitors influence access to the resource through some form of behavioral or chemical interaction between individuals prior to actual use of the resource. For example, both territorial behavior in animal populations and allelopathy in plant communities restrict competitor access to a resource in a spatially defined area (Brown, 1964; Rice, 1974). Resources allocated to territorial defense help to ensure that certain initial substrate resources never become so reduced by competitors that the population can no longer survive or reproduce. Antibiosis is generally recognized as the principal mechanism of interference competition by which fungi exclude other organisms from potentially available resources (Brian, 1957; Park, 1967; Wicklow, 1981a; Fravel, 1988).

Cooke and Rayner (1984) suggest that it is inadvisable and misleading to use the terms exploitation and interference competition when considering competition among fungi. They argue that during resource depletion many mycelial fungi restrict the access

of others as a result of either efficient nutrient uptake through densely branching hyphal systems or via antagonism. Their statement clearly identifies exploitation competition as "efficient nutrient uptake" and interference competition as "antagonism." There is no disagreement that both mechanisms may operate simultaneously (Wicklow, 1981a).

Cooke and Rayner (1984) also point out that a hyphal network, by its physical presence alone, is capable of stopping fungal hyphae from invading the underlying substrate. For example, *Xylaria hypoxylon* forms pseudosclerotial plates on precolonized beech (*Fagus sylvatica*) blocks upon contact with the white rot fungus *Coriolus versicolor* (Rayner and Boddy, 1988). Until their physical removal, the pseudosclerotial plates were capable of stopping *Coriolus versicolor* hyphae from invading the beech block. Apparently, *Xylaria hypoxylon* was unable to form a second pseudosclerotial plate in active opposition to *Coriolus versicolor*. In this example of interference competition, competitor access to the resource was restricted by *Xylaria hypoxylon*.

Enlightened interpretation of the adaptive behaviors of wood decay fungi should invite new research on the chemical signals and genetic regulatory mechanisms that enable a fungus to switch among growth forms effective in exploration, primary resource capture, or defense (Rayner and Boddy, 1988). Odum (1971, p. 32) recognized that organic substances released into the environment during decomposition may have profound effects on the growth of other organisms in the ecosystem, "...extracellular metabolites and waste products may be important chemical regulators which coordinate units of the ecosystem and help explain both the equilibria and the succession of species." For example, allelochemicals may coordinate late successional species in planktonic communities by serving as cues that trigger physiological responses in receptor organisms to an improving or deteriorating environment (Lewis, 1986). This allelochemical-signal hypothesis credits phytoplankton cells with physiological recognition mechanisms, implying that cells have evolved a certain amount of physiological programing based on allelochemical cues. It seems likely that fungi may also be genetically programmed to respond to decomposition products, antibiotics or volatiles generated within their natural microhabitats.

ANTIBIOSIS

Soil microhabitats in which nutrients are abundant, such as those associated with freshly incorporated organic detritus and seed or root exudates, are recognized as sites where antibiosis may occur in nature (Brian, 1957; Brock, 1966; Wicklow, 1981a). In such microhabitats, antibiotics produced by an initial fungal colonist may act to exclude other potential colonists. The literature of phytopathology is rich with examples showing an association between diminished growth or lack of pathogenicity by a soilborne root-infecting fungus in response to the antagonistic properties of certain saprophytic fungi from the rhizosphere (Baker and Cook, 1974; Cook and Baker, 1983; Fravel, 1988). Antibiotics produced by ectomycorrhizal fungi may act as a chemical barrier protecting tree roots against phytopathogens such as *Fusarium oxysporum* or in limiting access of other ectomycorrhizal species (Duchesne et al., 1989; Kope and Fortin, 1989, 1990; Marx, 1973; Paulitz and Linderman, 1991).

Some fungi that demonstrate antagonism to root-infecting fungal pathogens when paired in laboratory culture may or may not protect plants when applied as agents of biocontrol (Fravel, 1988). The rhizosphere environment may not support an antagonist population in large enough numbers to produce effective quantities of an antibiotic or the resources required for antibiotic production may differ among plant cultivars or soil

types. Proof that a given antagonism is due to the production of an antibiotic can be obtained only if the antibiotic is isolated and purified and the purified material is shown to have the same kind of activity against the test organism (Brock, 1966).

It should be noted that until recently (Thomashow et al., 1990) antibiotics had not been detected in rhizosphere soil (Williams and Vickers, 1986) and that previous 'observations' of antibiotic activity in the rhizosphere were based on indirect evidence. For example, prolonged saprophytic survival of a root-infecting fungus *(Cephalosporium graminearum)* in dead host tissues that were invaded during the parasitic phase of growth was associated with fungal ability to produce antibiotics (Bruehl et al., 1969). A UV-induced gliovirin-negative mutant of *Gliocladium virens* did not control *Pythium ultimum* on cotton seedlings as well as the gliovirin- producing parental strain (Howell and Stipanovic, 1983). Other mutants of *Gliocladium virens*, that were unable to parasitize *Rhizoctonia solani*, produced gliovirin and were able to suppress *Rhizoctonia*-induced damping-off of cotton in field soil (Howell, 1987). In a related example, production of the antibiotic chetomin by *Chaetomium globosum* in vitro was positively correlated with antagonism against the pathogen *Venturia inequalis* on apple seedlings (Cullen and Andrews, 1984). The authors considered this indirect evidence for antibiosis as the mechanism of antagonism. Duchesne et al. (1989) measured the "fungitoxicity of the rhizosphere" following inoculation with the ectomycorrhizal fungus *Paxillus involutus* as an indirect measure of antibiotic production.

The first isolation of an antibiotic (phenazine-1-carboxylic acid) from the rhizosphere of plants grown in natural soil was recently accomplished by Thomashow et al. (1990). Phenazine-1-carboxylate antibiotic-producing strains of *Pseudomonas fluorescens* 2-79 (NRRL B-15132) are more competitive in nature, as demonstrated by their ability to protect plant roots from a major root disease of wheat caused by *Gaeumannomyces graminis* var. *tritici* (Thomashow and Weller, 1988). Mutants defective only in phenazine synthesis, generated by transposon mutagenesis, were non-inhibitory to *Gaeumannomyces graminis* in vitro and substantially less effective in disease suppression in greenhouse tests.

Profesor Starmer and his colleagues are attempting to evaluate the role of killer yeasts in the organization of natural communities of yeast species associated with stem necroses of various cacti, slime fluxes of trees and decaying tissue of fruits (Starmer et al., 1987). Cactophilic killer yeasts such as *Pichia kluyveri* secrete proteins that are toxic to other yeasts (Zorg et al., 1988). Starmer et al. (1987) suggest that particular *Pichia kluyveri* genotypes may function in excluding other yeasts from the community. Here the mechanism of interference competition is clear and unambiguous.

Fungal toxins can prevent or reduce loss of resource or self to animals (Janzen, 1977; Wicklow, 1988). By characterizing seed-infesting toxigenic fungi as "seed eaters," Janzen has challenged microbiologists to broaden their ecological perception of such microorganisms to that of direct competitors of much larger seed-eating animals. He persuasively argues that because the seed-eating fungus faces losing both life and resource, such microorganisms are often under strong selection to render seeds as objectionable or unusable as possible to larger organisms in the shortest possible time. Janzen considered the toxic secondary metabolites produced by many seed-infecting fungi as analogous to chemical defenses of higher plants in that they serve to deter potential predators. Examples in which mycotoxins and other secondary metabolites produced by fungi could affect insects negatively have been reviewed by Wright et al. (1982) and Dowd (1991). The effects recorded include growth retardation, reduced pupal and adult size, lower fecundity, loss of fertility, increased mortality, repellency, and genetic changes.

Ecologists have asked whether antibiotics and other toxic secondary metabolites produced by fungi might offer some fungal species relative protection against potential predators, such as nematodes and arthropods, that consume soil and litter fungi (Whittaker and Feeney, 1971). Selective grazing by invertebrate mycophagists can influence the proportions of bacteria and fungi colonizing a resource and may affect the subsequent microbial succession and the rate of litter decay (Parkinson et al., 1979; Anderson and Ineson, 1984; Newell, 1984a, 1984b; Arsuffi and Suberkropp, 1985; Shaw, 1985 and this volume; Ingham, this volume). Fungi may allocate chemical defenses to protect structures critical to their survival, such as fruit bodies or sclerotia (Wicklow and Cole, 1982; Wicklow, 1988). Our investigations of these chemical defense systems has led to the discovery of new compounds showing significant anti-insectan activity (Wicklow et al., 1988; Gloer et al., 1988; Gloer et al., 1989; TePaske et al., 1989).

COLONIZATION STRATEGIES AND ANTAGONISM

Interference competition has probably been a selective force in guiding the evolution of fungal colonization strategies and in determining how different fungal populations become organized into communities. In recent years, mycologists have attempted to relate the behavior of populations of single fungal species to their colonization strategies, based on the system Grime (1979) developed for higher plants (Pugh, 1980; Cooke and Rayner, 1984; Widden and Scattolin, 1988; Andrews, this volume) and to apply the theory of r- and K-selection (MacArthur and Wilson, 1967) to the ecology of plant pathogens (Andrews and Rouse, 1982). Garrett (1970) had earlier associated some of the same behaviors for fungal substrate groups from soil that contribute to their "competitive saprophytic ability." Coates et al., (1981) recognized that "Genecological strategies" (Rayner, 1989) have also left their imprint on fungal community structure and resource use. Until recently mycologists had not fully appreciated the ecological implications of intraspecific mycelial interactions between thalli of different genotypes. Somatic incompatibility systems, can be strongly antagonistic and produce lytic reactions (Boddy and Rayner, 1982). Vegetative incompatibility not only contributes to the genetic variability in fungal populations but can also affect rates of substrate decomposition, as illustrated by the distinct zones of nondecayed wood separating adjacent colonies (Rayner and Boddy, 1988). It would be interesting to know if such hyphal compatibility reactions are important in determining the course of mixed-culture solid substrate fermentations (Wicklow, 1989). The physiological mechanisms producing these incompatibility reactions are unknown, but some form of premature hyphal senescence has been suggested (Rayner and Boddy, 1988). Premature hyphal senescence has also been associated with the phenomenon called "hyphal interference" (Ikediugwu et al., 1970; Ikediugwu and Webster, 1970a, 1970b). An even more rapid hyphal autolysis "fast lysis" is induced at short distances by volatiles of the mycoparasite *Pythium oligandrum* with its fungal host (Bradshaw-Smith et al., 1991).

In my earlier review (Wicklow, 1981a) I offered examples of how fungal antagonism might contribute to the organization of fungal communities, either by limiting competitor access to a resource or through species replacement. An effort was made to relate patterns of fungal colonization of natural substrates and models describing vegetational change in plant communities. The inhibition model of Connell and Slayter (1977) describes patterns of fungal colonization in which early colonists gain a foothold on a substrate, suppress the growth of others present, and inhibit the invasion of later colonists. According to Cooke and Rayner (1984) these species combine effective "primary

resource capture" (the sequestration of resources before they are taken by a competitor) with an ability to defend their "domain." Later successional species can invade and grow only when the dominating residents are damaged or killed, thus releasing resources. A competitive hierarchy, is a type of succession in which later successional plants are increasingly capable of dominating earlier successional species, as a regulatory process in determining the sequence of colonists in a successional sere (Horn, 1977). There are numerous fragmentary observations recorded in the mycological literature which suggest that (1) fungal antagonism may be an important mechanism of species replacement during substrate colonization and (2) such a competitive hierarchy may be operative in delimiting patterns of fungal colonization and sporocarp appearance (Wicklow, 1981a; Wicklow, this volume). Coates and Rayner (1985) and Chapela et al. (1988) also recognized that it is possible to place species of wood decay fungi which are dominant at different stages of community development into what they describe as a "combative hierarchy." The mechanism of species replacement may involve antibiosis (Wicklow, 1981a) and/or selective mycoparasitism (Rayner et al., 1987). Patterns of species abundance for a community of marine fungi colonizing submerged wood panels were also found to be associated with an organisms position in a competitive hierarchy, based on laboratory tests (Miller et al., 1985; Strongman et al., 1987). Miller (1991) is also credited for emphasizing ecologically relevant parameters in the design of fermentation environments that promote antibiotic production in marine fungi. By attempting to understand the relationship between the antagonistic properties of fungi and their ecological status in a community it may be possible to design relevant biocontrol strategies or guide the search for fungal metabolites with predictable biological activities (Wicklow, 1981a; 1988).

EXPERIMENTAL REQUIREMENTS

The importance of interspecific competition in the organization of biotic communities in nature is a subject that has stirred considerable recent debate among ecologists who differ in their "equilibrium" versus "stochastic" perspectives (Connell, 1983; Roughgarden, 1983; Schoener, 1983; Strong, 1983, this volume). Fungal ecology has a good deal to say about fungal competition, but has yet to contribute much to this debate. Might this be explained, in part, because the mycological literature is so foreign to ecologists who study large organisms, or because mycologists have not satisfactorily demonstrated that competition among fungi occurs in nature? Microbial ecologists are the first to recognize that, while it is important to find evidence for competition in natural ecosystems, it is also very difficult to study the competitive abilities of microbes in the natural environment (Alexander, 1971; Lacey, 1979; Veldkamp et al., 1984). Ecologists stress that empirical evidence for competition must come from field experiments in natural ecosystems where the historic occurrence of coevolution or interspecific competition is likely to produce communities in some state of equilibrium (Seifert, 1981; Starmer et al., 1987). The design of such field experiments is critical, and microbial ecologists should carefully consider these ecological criteria and assess the feasibility of applying such criteria to the organisms or systems they are studying. Ideally, a field experiment to demonstrate the occurrence of interspecific competition should measure the influence of interspecific competition on a population relative to that of other relevant processes affecting it, such as weather, predation, parasitism, mutualism, intraspecific competition, or disturbances (Connell, 1983). In such field experiments, the degree of exploitation or interference competition is experimentally manipulated by

changing the population densities of the competitors. Such a field experiment should involve changing the abundance of one potential competitor, species (A) followed by a comparison of the response (e.g., change in density, fecundity, or niche) of the other species (B) to its behavior in an unmanipulated control. If competition is affecting a species, there should be a statistically significant response in the opposite direction to the change in abundance of a potential competitor. A species may be self-limited, from the effects of the intraspecific competition, below the density necessary to eliminate a competitor. Therefore, to distinguish interspecific competition from intraspecific competition, the density of each species needs to be varied while keeping the density of the other species constant or removing it entirely (Connell, 1983; Schoener, 1983). Intraspecific competition was found to be stronger than interspecific competition in three out of four of the controlled field experiments in which it was judged that competition had been demonstrated (Connell, 1983).

Experiments, in which empty environments are created and the natural colonization of such environments is followed (i.e. fungal succession), do not provide an adequate measure of competition, because the competitors are not being manipulated directly (Schoener, 1983). The mycological literature offers numerous such examples of competition for substrate (i.e., cut stumps, surfaces of newly emergent leaves, buried cellophane or wheat straw, steam-sterilized greenhouse soil, etc.) (Tribe, 1966; Garrett, 1970; Wicklow, 1981b; Cook and Baker, 1983; Cooke and Rayner, 1984; Chung and Hoitink, 1990). Schoener (1983) is also critical of field experiments that claim to demonstrate interspecific competition when densities of competing populations are forced to levels higher than those occurring in nature. This occurs commonly in agricultural ecosystems when fungi are applied as agents of biocontrol (Rishbeth, 1963; Kommedahl and Windels, 1981; Papavizas, 1985). Strong (1983) points out that in ecological research, there may be simultaneous but different processes that give signals so similar that the products of individual phenomena are difficult to distinguish. He recommends use of the null hypothesis because it focuses on the pattern, outcome, or change one should expect if interspecific competition were not operating.

Unfortunately, none of the numerous and varied examples of fungal competition offered by Baker and Cook (1974), Cook and Baker, (1983); Cooke and Rayner (1984), Lockwood (1981) or Wicklow (1981a) could satisfy the necessary experimental criteria outlined by Connell (1983) or Schoener (1983) to demonstrate the occurrence of interspecific competition in natural ecosystems. However, a study involving lichenized fungi meets most of these requirements. Armstrong (1985) studied competition between foliose lichens growing on slate by using de Wit experimental design. Fragments of three species were cut from the edges of large lichen thalli and glued to pieces of slate in either monoculture or together in three mixtures of differing proportions, the density remaining constant in each treatment. After three years of continuous field exposure, the area of each species was used as an estimate of growth. *Parmelia conspersa* showed a significantly greater growth rate in monoculture and proved to be the dominant competitor in communities with either *Parmelia glaratula* or *Physcia orbicularis*. Colony-forming units representing potentially competing species of bacteria or fungi might similarly be applied to the exposed surfaces of leaves or plant litter, and their comparative growth and reproductive rates could be determined in situ.

Coprophilous fungal communities are particularly well suited to ecological experiments on fungal species competition and resource use (Yocom and Wicklow, 1980; Wicklow and Yocom, 1981; Wicklow, this volume). Numbers of fungal sporocarps/ spores produced on dung surfaces can be used as a measure of species fitness and com-

petitive ability. However, to determine if competition is occurring between two fungal species, one should attempt to vary initial spore densities within the fecal pellets experimentally. Whether other fungal communities can serve as experimental systems for demonstrating the relative importance of competition will depend on the ingenuity of mycologists in designing field experiments that adhere to the rigorous experimental criteria described.

CONCLUSIONS

Interference competition results from both interspecific and intraspecific mycelial interactions, or from interactions between fungi and larger oganisms (i.e., fungivorous arthropods) for the same resource. Examples provided above show how fungal antagonism has affected the organization of fungal communities, either by limiting competitor access to a resource or through species replacement. However, empirical evidence for competition in natural ecosystems, based on strict ecological criteria, is wanting. Understanding the relationships between the antagonistic properties of fungi and their ecological status in a community can enable one to develop effective strategies for biological control or to focus a search for fungal metabolites targeted against specific competitors and pest organisms.

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